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NOTES ON SOME PROBLEMS OF ADAPTATION.

2. ON THE TEMPORAL RELATIONS OF ASEXUAL PROPAGATION AND GAMETIC REPRODUCTION IN COSCINASTERIAS TENUISPINA: WITH A NOTE ON THE DIRECTION OF PROGRESSION AND ON THE SIGNIFICANCE OF THE MADREPORES.¹

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I.

Some time ago I gathered evidence showing that in the common Bermuda starfish, *Coscinasterias tenuispina* (Lamk.), there is unmistakable evidence of asexual multiplication through spontaneous division of the body into two parts (Crozier, '15). The modal number of rays in the adults of this species is 7²; the parts resulting from self division commonly constitute either 3 or 4 rays; each of these parts most usually produces 4 new rays. I may give here some additional data obtained in subsequent years, leading to the same conclusion (Fig. 1, Table I.).

TABLE I.

THE RELATION BETWEEN THE NUMBER OF LONG AND THE NUMBER OF SHORT RAYS IN 237 COSCINASTERIAS, OF WHICH EACH INDIVIDUAL HAD TWO DISTINCT GROUPS OF RAYS.

The table shows that as a rule 4 short rays are found in association with either 3 or 4 long rays.

LONG RAYS

SHORT RAYS.	1	2	3	4	5	6	7	
	1		1	1	5	5	3	15
	2		6	5	8			19
	3	2	18	32	5			57
	4	8	42	55	4			109
	5	7	17	7	1			32
	6	1	3		1			5
	1	20	84	100	24	5	3	237

¹ Contributions from the Bermuda Biological Station for Research. No. 121.

² It is entirely probable that here, as in *Solaster* (Gemmill, '12) and in *Lep- tasterias* (Osterud, '18), the fundamental ray number is 5, to which at an early age a sixth and, later, a seventh ray are normally added (cf. Crozier, '15).

The ordinary, gametic reproduction of these starfishes takes place in January–February. During summer months they are quite abundant under stones along the shore, just under low-water level. As winter approaches, they retreat for the most

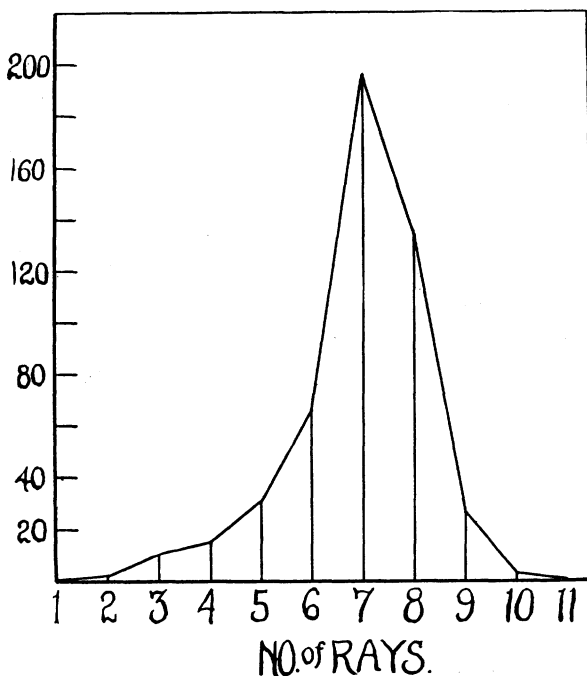


FIG. 1. The ray-frequency polygon derived from counts of 487 *Coscinasterias*. The essential characteristics of this curve are identical with those of a curve previously published (Crozier, '15).

part to somewhat deeper water, it would appear. In January and February, however, they crowd up to high-water mark, even on exposed shores, within Great Sound at least, and in Harrington Sound.³ Often they are consequently left high above water level

³ The question presents itself as to the possible rôle of phototropism in such shoreward movements. *C. tenuispina* is photonegative toward strong light, photopositive toward weak light; it is probable that these animals become photopositive toward slightly greater illuminations with lower temperatures. This might play some part in determining movements into more illuminated areas during the winter season; presumably gonadic secretions might also be involved. Plessner ('13) came to the conclusion that the "eye-spots" of starfishes enable these creatures to respond to the *direction* of light; in *C. tenui-*

when the tide recedes. Since they are not strongly photopositive, they are seldom exposed to the drying action of the sun, and survive the temporary absence of water. Occasionally they have been found killed by rain (this has also been seen with *Stichopus mæbii*).

I always noticed that in the breeding months the proportion of animals which seemed to have recently undergone self division was much less than during the summer. Some attempt was therefore made to discover the percentage of recently divided specimens obtainable in each month of the year. This was done, somewhat unsystematically, for several years. The result is set forth in Table II. The data for each two-month period might have been averaged together, thus perhaps obliterating to some

TABLE II.

THE PERCENTAGE OF "NON-REGENERATING" COSCINASTERIAS SECURED IN
RANDOM COLLECTIONS DURING EACH MONTH, 1915-1918.

Period.	Total No. of Individuals	Not Recently Di- vided,—Per Cent-
January	74	59
February	60	63
March	35	60
April	30	40
May	34	17
June	18	11
July	113	12
August	74	33
September	40	20
October	32	41
November	27	33
December	20	75

extent the possible variation from year to year. The numbers in the last column of the table express for each period the percentages in which the rays were 5 to 9 in number and of approximately equal length—in other words, those which exhibited no evidence of reasonably recent self division.

For June-July-August, 1913 and 1914, I found (Crozier, '15) 83.6 per cent. of the individuals to exhibit a group of longer and *spina*, however, the tips of the rays shorten noticeably when a shadow is cast on them alone, whereas in sunlight the tips of the rays tend to be curled upward.

a group of shorter rays. In the same months of 1915-1918, the percentage was 80.4, a sufficiently good agreement. This is about the maximum percentage of regenerating, or recently divided, individuals encountered during a twelve-month period. From Fig. 2 it is evident that the highest percentage of intact specimens not recently divided occurred during December to March

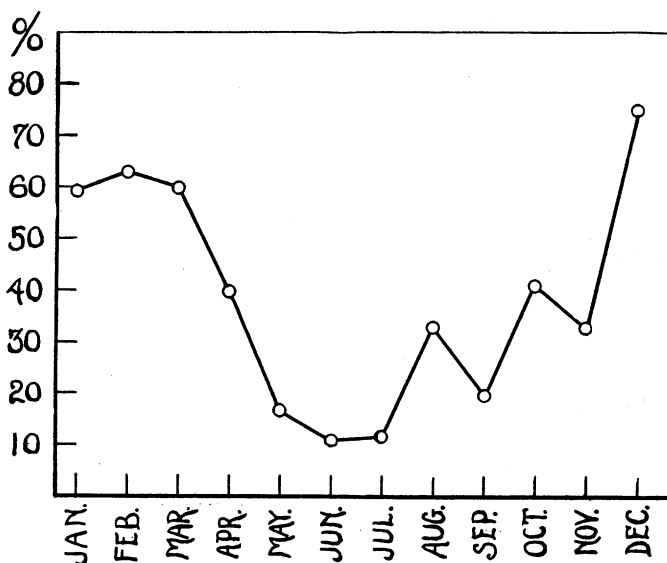


FIG. 2. The average percentage of *Coscinasterias* not showing evidence of recent self-division, during each month (1915-18).

—the percentage then rather rapidly sinking to a minimum during midsummer.

There is a certain correlation between the course of the curve of self-division (Fig. 2) and that of temperature-variation in the sea water. I reproduce here a seasonal temperature graph derived from figures given by Verrill (1902), together with the averages of my own data; the curves agree rather well, in spite of the fact that my temperature readings were not very numerous, nor systematically taken, but were obtained mainly for different special purposes having to do with other problems.

In comparing Figs. 2 and 3, it must be recalled that the "curve of self-division" is non-quantitative in one important respect: the percentages of dividing animals include data derived from indi-

viduals which may have divided some little time previous to others, as indicated by the various stages in regeneration classified under this head. A "lag" in this curve of division with respect to water temperature might therefore be expected. The sudden rise of percentage of "non-regenerating" specimens at December, however, is probably adequate proof that a month or so is sufficient time for the full growth of new rays. The actual "lag" in the curve of autotomy is of the wrong sort for the idea

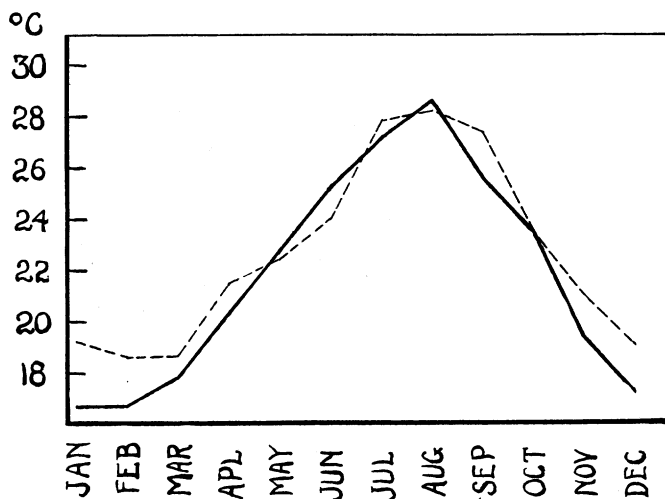


FIG. 3. Mean monthly temperatures of seawater at Bermuda. Heavy line, data from Verrill ('02); dotted line, averages from records of W. J. C. The dotted line records for winter months are higher than those given by Verrill, probably because my own observations were restricted for the most part to the waters of the partially enclosed Sounds.

of complete temperature control, because the decrease in frequency of self-division perceptibly precedes the seasonal decrease of temperature. This might be explained on the basis that the onset of higher temperature in spring serves indirectly to induce self-division, but that the capacity for this method of propagation is gradually exhausted, or in some fashion checked, before the warmer season has closed.

It is interesting, however, to notice how the frequency of self-division is enormously decreased at the approach of the period of breeding. There is thus accomplished, whether through the

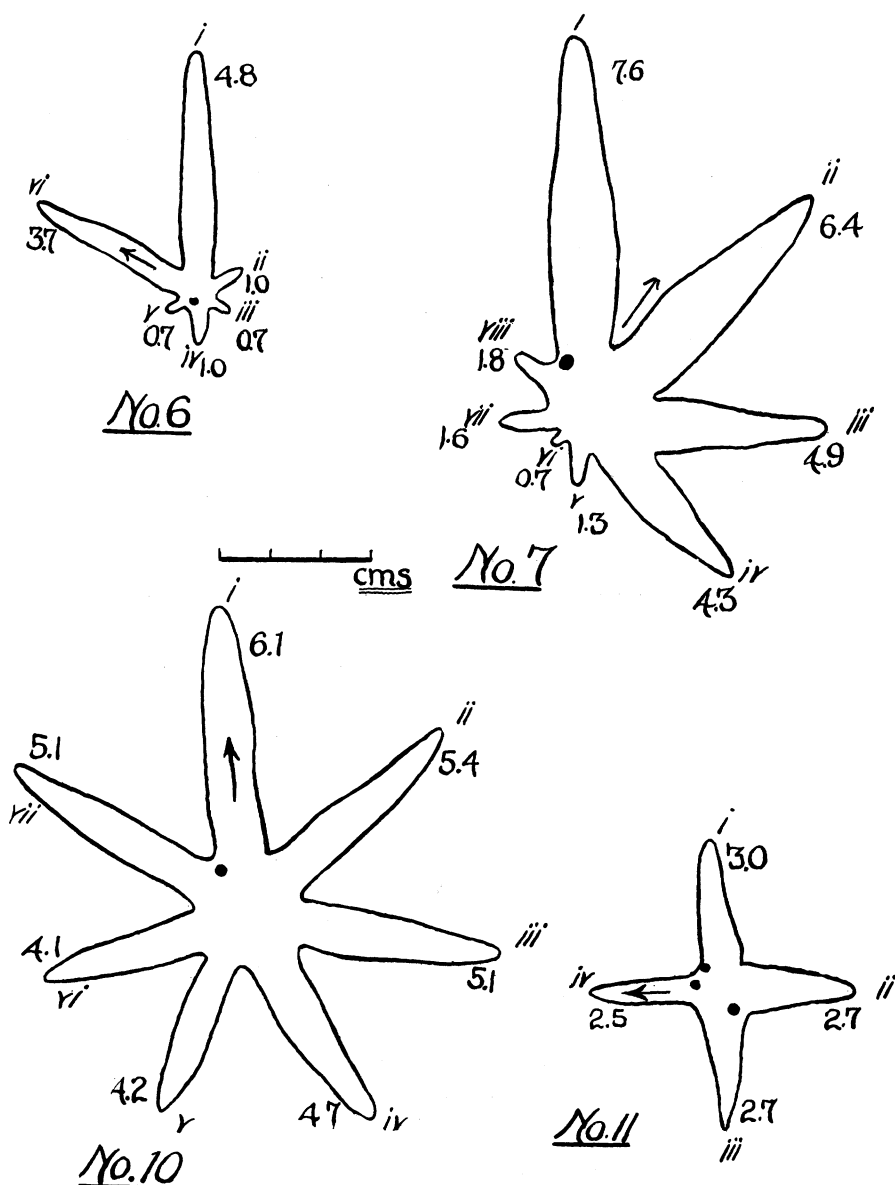


FIG. 4. The direction of progression (arrow) in two typical instances of recently autotomized halves of *Coscinasterias*. a, division surfaces; non-directive stimulation.

agency of temperature or in some other way, a nice adjustment of the two dissimilar methods of multiplication practiced by this species. Asexual increase through self-division of the body is at a minimum just before and during gametic reproduction. It is not difficult to suppose that an undivided individual is better suited for gamete formation and for such coördinated movements as probably are concerned in bringing the sexes near together for fecundation of the eggs. The general energy of the animal is then directed toward the elaboration of gametes, rather than diverted to the formation of new tissue. To what extent the elements of this correlative mechanism are causally related, however, one must refrain from guessing. Judging from the statements of Clark ('13a, '13b) and Mortensen ('17) regarding the asexual multiplication of *Linckia guildingii*, and the period of its egg-reproduction, I suspect that the supplementary relation here pointed out for *Coscinasterias* may not obtain with *Linckia*, where, however, the method of self-division is different, consisting not in the division of the body across the disc but in the abstriction of a portion of a ray. Nor in *Holothuria surinamensis* is there good evidence of an alternation of the sexual and asexual methods of multiplication (Crozier, '17).

II.

The number of madrepores in *Coscinasterias* is quite variable, from 1 to 5 being found on a disc. As earlier suggested (Crozier, '15), the number of madrepores is correlated rather definitely with the total number of rays (Tables III., IV.). It was observed that during the addition of new rays, subsequent to self-division, one or more new madrepores are also added. In almost every case, throughout the several hundred carefully examined, each moiety of a divided body bore one or several "old" madrepores. Moreover, some of the very largest specimens collected, with ray lengths of 12-13 cms., had but 5, 6, or 7 rays, of equal length, with but *one* madrepores. These facts suggested that the development of several madrepores is perhaps a more or less necessary preliminary to normal self-division. The madrepores are usually formed at widely separated points on the periphery of the disc; hence the probability is that each part of an

animal, when the creature divides, will carry at least one of these bodies.

TABLE III.

THE CORRELATION BETWEEN NUMBER OF MADREPORES AND NUMBER OF RAYS IN A RANDOM SAMPLE OF 275 COSCINASTERIAS.

Note that one or several madrepores are always present on the parts of recently bisected (autotomized) individuals.

NO. OF RAYS.

MADREPORES.		2	3	4	5	6	7	8	9	10	
	1	2	5	4	5	13	21	10	2		62
	2		2	4	5	10	25	14	3	2	65
	3					6	29	30	2		67
	4					5	18	28	4		55
	5				1	1	2	4			8
		2	7	8	11	35	95	86	11	2	257

TABLE IV.

THE CORRELATION BETWEEN NUMBER OF MADREPORES AND NUMBER OF RAYS, AMONG 82 COSCINASTERIAS SELECTED SO AS TO INCLUDE ONLY INDIVIDUALS IN WHICH ALL THE RAYS WERE OF VERY NEARLY EQUAL LENGTH.

One or several madrepores commonly appears at the edge of the disc where rays are being newly added, subsequent to a self-division.

NO. OF RAYS.

MADREPORES.		3	4	5	6	7	8	9	
	1	4	2	3	5	11	1	1	27
	2	1	2	3	2	5	2	1	16
	3		1		2	14	6		23
	4				3	8	4	1	16
		5	5	6	12	38	13	3	82

Cole ('13) discovered that *Asterias forbesi* tends to creep in such a way that, in the absence of directive stimuli, the portion of the animal nearest to the single madreporite is usually in advance—a true, though subordinate, “physiological anterior.” He suspected that the water-system might be concerned in some way with the determination of this “anterior.” The conditions in *Coscinasterias* might perhaps be regarded in one, or both, of these two ways: (1) there is a physiological basis for the development of one or several madrepores according to the number

of rays, *i.e.*, depending on the total water requirements of the locomotor organs; or (2) the multiplicity of madrepores is adaptively related merely to the habit of self-division. At first I was inclined to entertain the former idea; the fact, however, that 7-, 8-, and 9-rayed individuals, as well as those of 5, 6, or 7 rays and of large size, do get along quite well with a single madre-pore is more favorable to the second notion.

I would regard it as possible, then, that the multiplication of madrepores at separated points on the disc of *Coscinasterias* furnishes merely an assurance that portions of the body separated by autotomy will each be provided with a madreporic canal. It is not improbable, however, that the very development of supernumerary stone-canal, by furnishing each an additional "physiological anterior point,"—such as that revealed by Cole's ('13) experiments with *Asterias*,—provides automatically the very conditions determining self-division.

III.

The probability of this explanation of the significance of the madre-pore might be tested by determining the direction of progression in various individuals, under non-directive stimulation. I studied from this standpoint the locomotion of 12 *Coscinasterias*. Non-directive conditions were secured very much as in Cole's ('13) experiments: an 8-c.p. filament, the only source of light, was suspended in the axis of a circular aquarium tub 3 feet in diameter, and 4 feet above the surface upon which the starfish crept. The tub held sea water to a depth of 10 cms. One half hour elapsed between trials. The observations were made at night. To horizontal light of this intensity, *Coscinasterias* was slightly photonegative, but more intense illumination was required to cause decided negative movements. Even under the supposition that illumination of a larger ray might lead to the determination of directed photonegative movements when the animal is illuminated vertically, owing to the larger sensory surface of such a ray, the conditions here established must be regarded as essentially non-directive, because the starfishes often crawled with some other than the longest ray *in advance*.

The length of the rays and the number of madrepores pre-

senting such great variations, it was possible to obtain a fairly definite idea of the relative values of *ray-length* and *madrepore-position* as determiners of the "physiological anterior"; for *Coscinasterias* does show definite tendencies in the orientation of its body with respect to creeping. Since the organization of the body of this starfish is somewhat irregular, the observations cannot be summarized in terms of morphologically defined rays (I did not note the position of the anal opening in these cases; cf. Gemmill, '14). I must therefore give several instances in detail (Table V.).

TABLE V.

SHOWING THE NUMBER OF TIMES EACH RAY OF THE STARFISHES ILLUSTRATED IN FIGS. 4 AND 5 WAS USED AS "DIRECTOR."

No. of the Animal.	No. of Trials.	Ray.								
		i.	ii.	iii.	iv.	v.	vi.	vii.	viii.	ix.
1	33	8	18	0	5	2				
2	24	10	10	1	1	1	1			
3	30	8	3	2	0	1	8	2	0	6
4	16	15	0	0	0	0	1			
6	16	1	0	0	3	0	12			
7	15	7	8	0	0	0				
10	16	8	0	0	0	0	4	4		

In the creeping of *Coscinasterias*, which is rather slow (at 24°, about 12-15 cms. per min.), several points are similar to ones emphasized by Cole in *Asterias*, notably the tendency to exhibit a definite region as "physiological anterior," with, however, clear evidence of the "rotation" of this anterior.⁴ A good instance of such rotation is the following:

Coscinasterias No. 1, September 9, 1915. Creeping under vertical light, the region in advance shifted slowly, in this order (cf. Fig. 5): i, i, ii, ii-i, ii, ii, iii, iii-iv, v-iv, the animal being undisturbed from the outside.

Such "rotation of the impulse" was observed to be either clock- or anticlockwise. Ordinarily rotation of this sort was not

⁴ Agersborg ('18), in describing the righting movements of the "twenty-rayed" *Pycnopodia helianthoides*, has spoken of "bilateral tendencies" in the activities of this starfish. But the condition of his tests are not well specified, nor is there any indication given of a relation between the "bilaterality" and structural conditions in *Pycnopodia*.

conspicuous, so that a fairly definite region could be distinguished as an "anterior" in creeping. From the typical records submitted, it appears that as a rule either the longest ray, or a long ray near a madrepora, is the "directive" ray.

As to the relative importance of ray-length and position of madrepora, it seems clear that, although no absolute rule can be

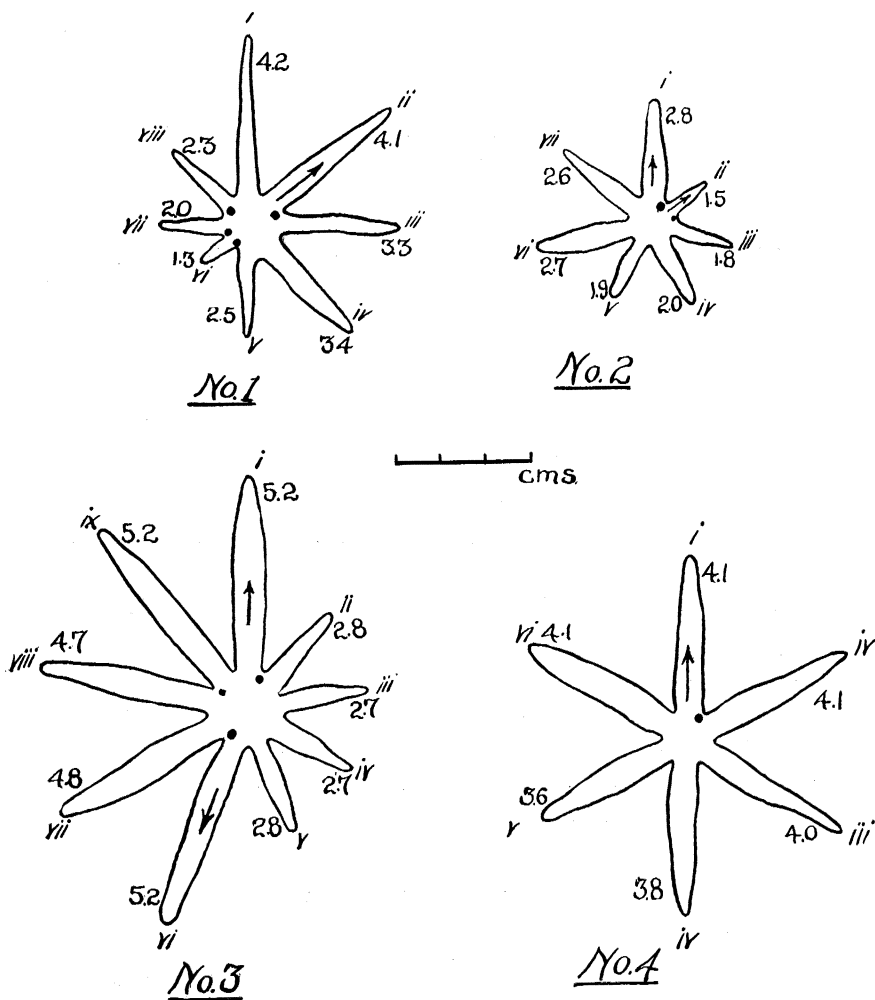


FIG. 5. Figs. 4 and 5 show typical instances of the "physiological anterior" in *Coscinasterias* (see Table V); i, ii, . . . , numbers assigned to rays; lengths of rays in cms.; madrepores, black; predominant directions of locomotion under non-directive stimulation shown by arrows.

stated, the latter factor is, on the whole, preponderant.⁵ In 13 cases, where the disposition of rays and of madreporites was most favorable, the *longest ray* was recorded as "director," in the average, for 32.2 per cent. of the trials; a *ray near a madreporite* being so recorded, in the average, for 42.2 per cent. of the trials.

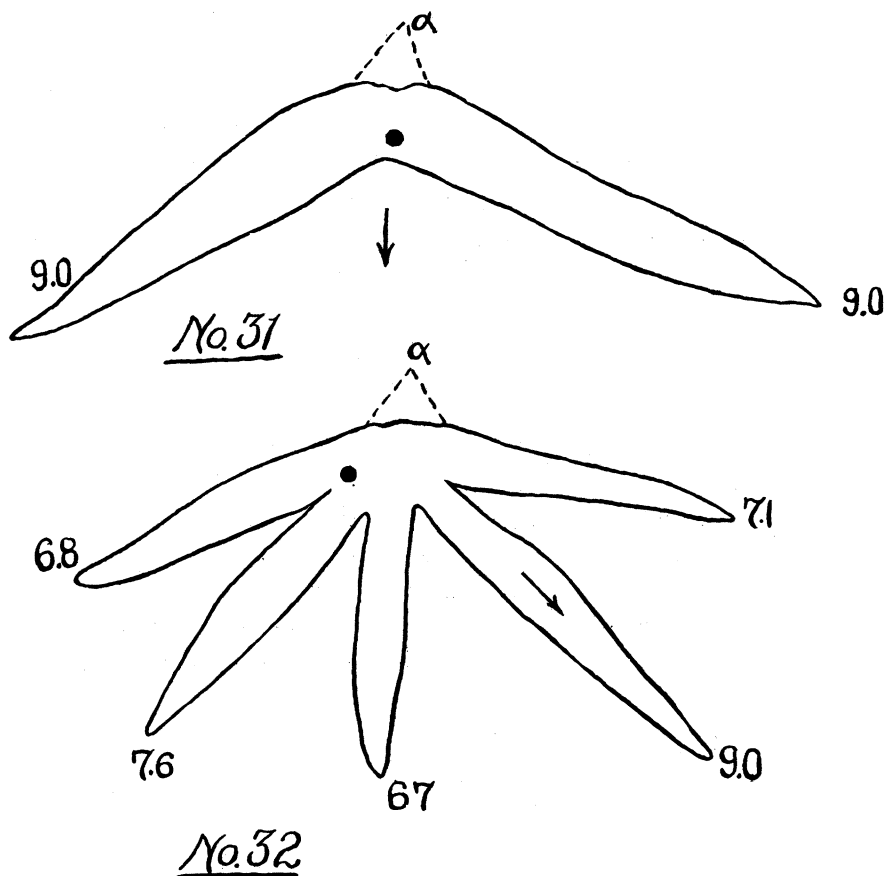


FIG. 6. The direction of progression (arrow) in two typical instances of recently autotomized halves of *Coscinasterias*. α , division surfaces; non-directive stimulation.

More convincing than such averages, however, are the actual data already set forth.

Frequently, in the case of animals having two ray-groups

⁵In connection with the matter of physiological and anatomical polarity in echinoderms, compare Clark's observations on the locomotion of *Comatula purpurea* ('15, p. 112), and mine on the creeping of *Mellita* (Crozier, '20); in both forms there is clear evidence of functional bilaterality.

greatly differing in size, the directive ray appears to be one next to the plane of antecedent autotomy. This fact might seem unfavorable to the conception of the "cause" of autotomy above formulated, but in fact I found that if the creeping of halves of starfishes recently separated was studied, the results were, on the contrary, favorable to this conception. Examples in point are afforded by such specimens as are illustrated in Fig. 6.

IV.

Summary.—It has been pointed out that in those individuals of *Coscinasterias tenuispina* which divided autotomously more than one madreporite is developed on the disc previous to division. Further, that each madreporite, or group of madreporites, is an external sign (at least) of the development of a tendency toward the establishment of a "physiological anterior" point, as expressed in creeping. Hence it is suggested that the cause of the autotomous separation of the body of this starfish into two approximately equal parts—each as a rule then automatically receiving one or more madreporites—may be intimately connected with the very development of these structures. It is shown that this asexual multiplication by self-division exhibits a seasonal rhythm so adjusted as to constitute a propagative method which supplements, in point of time as well as in kind, the ordinary gametic reproduction, the former method being distinctly in abeyance during the winter months (January–February), when breeding occurs.

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